

EXPLORING FUNCTIONAL ASSOCIATIONS BETWEEN SPIDER CRIBELLA AND CALAMISTRA

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ABSTRACT. A spider's calamistrum draws silk fibrils from its cribellum and helps combine them with supporting strands to form a cribellar prey capture thread. Despite the close functional association of these two features, this study shows that there is a great deal of variability in the ratio of cribellum width to calamistrum length. When the independent contrast method was used to examine these two features in 11 species representing seven families, no relationship was found. Likewise, no relationship was found among nine species representing seven genera of the family Uloboridae. Only among the 14 species of *Mallos* (Dictynidae) was calamistrum length directly related to cribellum width. This suggests that, above the genus level, differences in spinning behavior and morphological features such as leg length and abdomen size and shape influence the relationship of these two features.

Keywords: cribellar thread, cribellate spiders, independent contrast method, functional linkage

The outer surfaces of a cribellar capture thread are formed of thousands of fine, looped fibrils that are produced by spinning spigots on the cribellum (Eberhard & Pereira 1993; Opell 1994a, 1995, 1996; Peters 1983, 1984, 1986, 1992). These fibrils are drawn from the cribellum and manipulated by a setal comb on the fourth walking leg, termed the calamistrum, as they are combined with axial and, in some cases, paracribellar fibers to form a completed capture thread. This close functional linkage between the calamistrum and the cribellum suggests that their features should also be closely related. The most obvious features to exhibit this relationship should be calamistrum length and cribellum width. We predict that the calamistrum must be long enough to fully span the cribellum as it sweeps over it in a combing motion. However, cribellum width may not be the only factor that influences calamistrum length. The effective length of a calamistrum is probably determined by such factors as the angle at which the calamistrum passes over the cribellum and the lateral movement of the calamistrum during a combing stroke. Although these features

and their relationships are poorly studied, they are likely to be affected by the length and width of a spider's abdomen, the length of a spider's fourth legs, by the manner in which the combing leg is supported (Eberhard 1988), and probably by other details of the combing behavior such as the length of each combing stroke.

The diversity in cribellar thread-combing behavior documented by Eberhard (1988) suggests that the ratio of calamistrum length to cribellum width may differ considerably among cribellate taxa. The null hypothesis of this study is that this ratio is uniform for all cribellate taxa. Using the comparative method of phylogenetic systematics (Harvey & Pagel 1991), we test this hypothesis at three hierarchical levels: the interfamilial level, the intrafamilial level, and the intrageneric level. The degree to which differences in behavior and other aspects of anatomy influence the ratio of calamistrum length to cribellum width will affect the level at which the null hypothesis will be rejected. As behavioral and morphological features should be most similar within members of the same genus, it should be more difficult to reject the null hypothesis at this level than at more inclusive levels.

METHODS

Measurements.—The fourth legs and cribella of spiders were removed and mounted in water-soluble medium on microscope

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Table 1.—Means and standard deviations of the ratio calamistrum length to cribellum width of representative species.

Family Species	<i>n</i>	\bar{x}	SD
Uloboridae			
<i>Miagrammopes animotus</i>	31	1.35	0.10
<i>Uloborus glomosus</i>	21	1.10	0.13
<i>Octonoba sinensis</i>	24	1.27	0.11
Dictynidae			
<i>Mexitilia trivittata</i>	6	1.67	0.24
<i>Mallos bryantii</i>	5	1.55	0.25
<i>Mallo niveus</i>	9	1.58	0.27
<i>Mallos mians</i>	8	1.49	0.19

slides. Calamistrum length and cribellum width were measured to at least the nearest 20 μm under a compound or dissecting microscope. Two indices can be used for calamistrum length: the distance separating the tips of the proximal and distal-most setae of the calamistrum and the distance separating the proximal and distal-most setal bases. We chose the second index for two reasons. First, it can be more consistently measured and is not affected by missing setae. Second, it does not make any assumptions about the deflection of calamistrum setae during cribellar fibril combing. In the case of those species with divided cribella, cribellum width included the central region that separated the two halves of the cribellum. We measured a single mature female per species. We reasoned that, as the cribellum and calamistrum must be functionally linked throughout an individual's development, these measurements would provide a more rigorous test of the hypothesis than would the use of mean values derived from several individuals of a species. Table 1 gives the variance of the ratio of calamistrum length to cribellum width for seven species included in this study.

Phylogenetic analysis.—This study includes representatives of the infraorder Araneomorphae, the family Uloboridae, and the dictynid genus *Mallos* O. Pickard-Cambridge 1902 (Figs. 1–3) and uses the phylogenies of Griswold et al. (in press), Coddington (1990), and Bond & Opell (1997), respectively. To analyze the relationships of calamistrum length and cribellum width in a phylogenetic context we used the independent contrasts method of

Felsenstein (1985), as implemented by the Comparative Analysis of Independent Contrasts program of Purvis & Rambaut (1995). All branch lengths were treated as equal. This method minimizes the influence of non-independence of the data due to phylogenetic relationship by analyzing directional changes in continuous characters. It does so by computing differences between the features of sister taxa (both extant taxa and their inferred ancestors). These differences are then normalized and relationships among the resulting independent contrast values are examined using regression statistics (see Harvey & Pagel 1991 for a review of this approach).

All known species of the genus *Mallos* were included in the analysis of the relationship between the calamistrum length and cribellum width. In contrast, analyses of the other two clades included only some of the known members. We examined the consequences of partial sampling by analyzing the relationship between calamistrum length and cribellum width within subsets of the genus *Mallos*. We used a random number generator to select seven of the 14 species of *Mallos*. After constructing a pruned phylogeny that included these seven species and *Mexitilia trivittata* (Banks 1901) as an outgroup, we ran an independent contrast analysis for calamistrum length and cribellum width. This procedure was repeated until a total of ten analyses had been run. We then repeated the entire procedure a second time with nine species of *Mallos* being selected each time.

RESULTS

Values for calamistrum length and cribellum width are given in Figs. 1–3. Within the Araneomorphae, the ratio of calamistrum length to cribellum width ranged from 0.99–2.57; and an independent contrast analysis showed that there was no relationship between the dimensions of these two features ($F = 0.09$, $R^2 = 0.01$, $P = 0.77$). Within the Uloboridae the ratio of calamistrum length to cribellum width ranged from 1.07–2.06 and an independent contrast analysis showed that there was no relationship between the dimensions of these two features ($F = 0.63$, $R^2 = 0.10$, $P = 0.46$). When this analysis is restricted to orb-weaving uloborids of the genera *Waitkera* Opell 1979, *Siratoba* Opell 1979, *Uloborus* Latreille 1806, *Octonoba* Opell

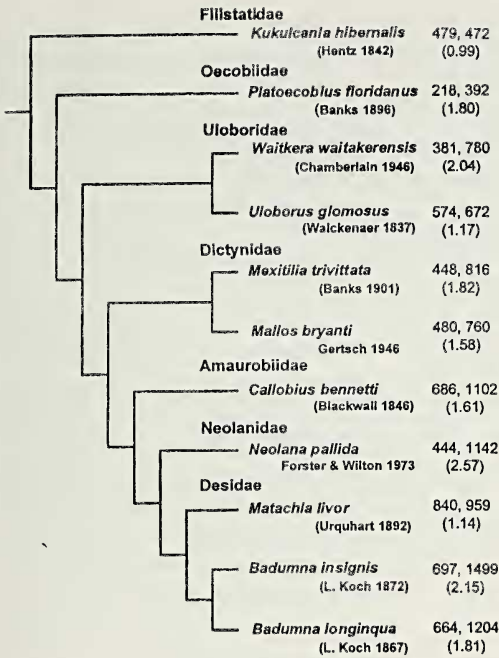


Figure 1.—Phylogeny of species representing seven families (from Griswold et al. 1999). Following each species is the width of its cribellum and the length of its calamistrum, both in μm. Ratios of calamistrum length to cribellum width are in parentheses.

1979, and *Philoponella* Mello-Leitão 1917 an independent contrast analysis still fails to show a relationship between calamistrum length and cribellum width ($F = 0.11$, $R^2 = 0.05$, $P = 0.77$).

Within the genus *Mallos*, the calamistrum length to cribellum width ratio ranged only from 1.26–1.82 and an independent contrast analysis showed that there was a relationship ($F = 8.40$, $R^2 = 0.41$, $P = 0.013$) between the dimensions of these two features (Fig. 4). However, in only three of the ten subsets that included seven *Mallos* species plus *Mexitilia trivittata* was there a significant relationship between calamistrum length and cribellum width ($F = 8.91$ – 22.75 , $R^2 = 0.64$ – 0.82 , $P = 0.005$ – 0.031). When the sample size was increased to include nine *Mallos* species, seven of the ten samples showed a relationship between these features ($F = 5.61$ – 19.95 , $R^2 = 0.45$ – 0.74 , $P = 0.050$ – 0.003).

DISCUSSION

The size of a spider's cribellum and the number of spigots that it bears are the main

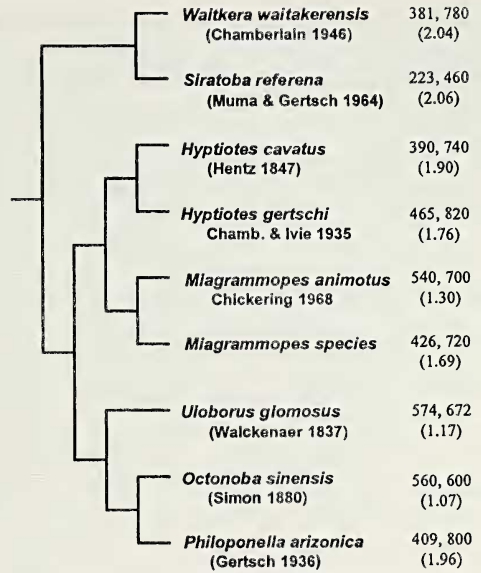


Figure 2.—Phylogeny of species belonging to the family Uloboridae (from Coddington 1990). Following each species is the width of its cribellum and the length of its calamistrum, both in μm. Ratios of calamistrum length to cribellum width are in parentheses.

factors that correlate with the stickiness of the cribellar thread that it produces (Opell 1994a, 1995, in press). However, differences in the way cribellar fibrils are combined with supporting fibers can alter thread stickiness (Opell 1994b), as can the deposition of linear cribellar threads in a looped manner when they are placed in the web (Opell, unpub. data). Although cribellum shape differs among taxa, spigot number is generally related to cribellum width. This evolutionary plasticity in cribellum width is reflected by differences in calamistrum length.

The ratio of calamistrum length to cribellum width differs among taxa; but, with one exception, it always exceeds one. In *Kukulcania hibernalis* (Hentz 1842) calamistrum length and cribellum width are essentially the same. This suggests that the production of a cribellar thread requires the calamistrum to span the complete width of the cribellum during a combing stroke. It is possible that a calamistrum could comb fibrils from only part of the cribellum spigots, but this seems unlikely for two reasons. First, as the spigots of the cribellum are probably not regionally controlled, non-calamistrum setae on other parts

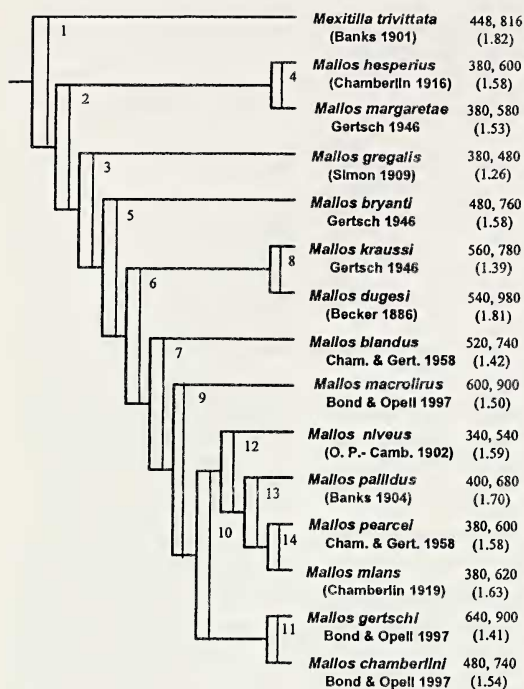


Figure 3.—Phylogeny of the 14 known species of *Mallos* and a representative of its sister group *Mexitilia* (from Bond & Opell 1997). Following each species is the width of its cribellum and the length of its calamistrum, both in μm . Ratios of calamistrum length to cribellum width are in parentheses. Numbers near vertical lines denote the sister groups whose independent contrasts are given in Figure 4.

of the combing leg that contacted cribellum spigots would tend to draw fibrils from them and these would become stuck to the leg or catch on the forming cribellar thread, thereby interfering with cribellar thread production. Second, cribellar thread is materially costly to produce (Opell 1997, 1998) and it seems unlikely that a cribellum with an unused lateral region would be retained. The apparent ease with which the cribellum itself is lost is documented by a number of families, genera, and even species pairs (putative sister species) that have both cribellate and ecribellate members (Forster 1970; Forster & Wilton 1973).

This study shows that at higher taxonomic levels, there is no uniform relationship between cribellum width and calamistrum length. This suggests that the angle at which a calamistrum passes over a cribellum or the amount of lateral movement of the calamistrum during a combing stroke differs greatly

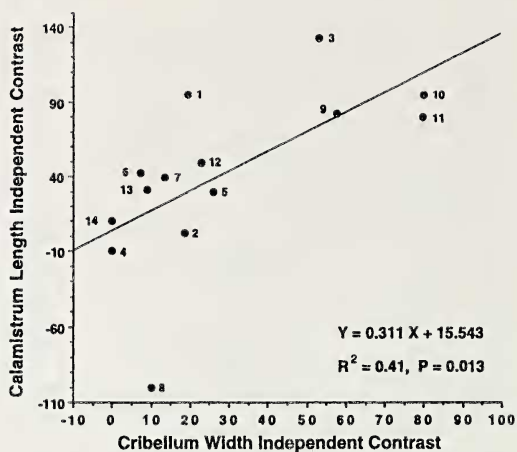


Figure 4.—Regression of independent contrast values for cribellum width and calamistrum length for 14 *Mallos* species and *Mexitilia trivittata*. Numbers identify the sister groups in Figure 3 from which these values were computed.

among spiders. As noted in the introduction, a variety of morphological and behavioral factors may influence the position and path of the calamistrum.

Even among orb-weaving species of the family Uloboridae that support the combing leg in the same manner (Eberhard 1988; Opell unpub. obs. for *Waitkera waitakerensis* (Chamberlain 1946), *Siratoba referena* (Muma & Gertsch 1946), *Uloborus glomus* (Walckenaer 1837), *Octonoba sinensis* (Simon 1880)) and share more similar body plans (abdomen dimensions, leg lengths, and ratios of leg articles; Opell 1979), the ratio of calamistrum length to cribellum width differs considerably. It is only within the genus *Mallos* that a clade-specific correlation between calamistrum length and cribellum width can be demonstrated. Even here this relationship is not exceedingly strong, as it begins to decay when sample size decreases.

As comparisons of calamistrum length and cribellum width within the family Uloboridae and among families are based on small samples, it is possible that an increased sample size would establish a significant relationship between these features. However, in comparisons of other spider features similar phylogenetic representation has been sufficient to demonstrate significant relationships (Opell 1994a, 1996, 1997, 1998, 1999, in press). Therefore, if there is a general relationship be-

tween calamistrum and cribellum features, it is weaker than those of other aspects of the phenotype.

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